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THE BIOMETRIC PROOF OF THE PURE LINE THEORY¹

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I. INTRODUCTION

ON this platform I find myself in a somewhat embarrassing position. A friend assured me in advance that this symposium would be somewhat analogous to the country parson's "praise service," and into this pure devotional atmosphere I must bring a note of agnosticism.

Agnosticism is a term selected after careful deliberation. Johannsen's propositions are important—if true—and any candid naturalist must hesitate before opposing a new theory which may lead to important advances in biology. Agnosticism is the condition of mind temporarily enforced by the results of my own experiments. If one is pledged in advance to the pure line theory many of these observations can be made to confirm Johannsen's conclusions. If one is unprejudiced and seeks to fit his theories to his observations, rather than to adjust his facts to his preconceived conclusions, the results are quite as capable of other interpretation. Possibly more extensive work may show clear confirmation of his results. Meanwhile I must withhold final judgment, merely stating that my own work has greatly shaken my confidence in Johannsen's theory.

Here I do not care to dwell upon details of my own experiments. It seems more profitable to try and state the fundamental problems of the pure line theory as they appear to the biometrician and to indicate the methods of work which seem to him necessary to the drawing of sound conclusions.

¹ From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

II. THE FUNDAMENTAL PROPOSITIONS OF THE PURE LINE THEORY

Our symposium has for its subject the Genotype or Pure Line Theory. Some of the speakers have enthusiastically urged us to replace the words "pure line theory" by "pure line facts." If this were done there would be little need for this program. Pure line facts are as yet a very insignificant part of biological data. The real occasion for this symposium is the pure line theory—the rank vines which have grown from the nineteen bean seeds which Johannsen planted in 1901. Biologists would have been little interested by the statement that selection within the offspring of a single bean has been ineffective in changing the weight of the seed. It is the daring generalization of the conclusions drawn from these limited experiments—the curt characterization of other researches as of no biological significance or their reinterpretation (from flounder's fins to intelligence in school children) in terms of the bean experiments, that forces us to take an interest in these matters.

Our first problem is to ascertain what these generalizations—the elements of the pure line theory as contrasted with the pure line facts—are. Our second task is to try to ascertain in how far experimental facts support the pure line theory.

Davenport² has given a particularly good outline of Johannsen's theory:

The fundamental principle of Johannsen is that an ordinary frequency polygon is usually made up of measurements of a characteristic belonging to a non-homogenous mass of individuals; that it is really analyzable into several elementary masses each of which has a "frequency polygon" of its own. In each elementary polygon the variation is strictly due to non-inheritable somatic modifications, selection of extremes of which has no genetic significance. But the selection for breeding of individuals belonging to different elementary polygons, lying, say, at the extremes of the complex, may quickly lead to an isolation of these elementary polygons, the constituent individuals of which reproduce their peculiarities as distinct elementary species.

² Davenport, C. B., *Science*, n. s., 30: 852, 1909.

We recognize three essential propositions:

Proposition 1.—Most species or varieties are not homogeneous, but are composed of a large number of minor forms.

The series of individuals classified as the same variety or race by the systematist, regarded as homogeneous material for experiment by the physiologist, lumped together to form a single "population" by the statistician, is designated by Johannsen as a phænotype. This phænotype may generally be analyzed by pure line breeding into many constant and indivisible strains known as genotypes.

Systematists have long regarded certain groups as polymorphic. *Aster*, *Rubus*, *Salix* and *Cratægus* at once occur to the botanist and *Unio*, *Salmo* and the staphylinids to the zoologist. But the genotype theory seems to regard systematic polymorphism as a much wider phenomenon. Indeed one is sometimes assured that every apparently uniform cultivated variety is a swarm of constant biotypes. Johannsen emphasizes the generality of heterogeneity. For instance, he says:³

Ein gegebener Phaenotypus mag Ausdruck einer biologischen Einheit sein; es braucht es aber durchaus nicht zu sein. Die in der Natur durch variationsstatistische Untersuchungen gefundenden Phaenotypen sind es wohl in den allemeisten Fällen nicht!⁴

Again on page 162:

In der Praxis wirkt ein Selektion meistens schnell in der beabsichtigen Richtung—eben weil die Bestände oder Populationen fast immer Gemische sind.

One more illustration will suffice:

Der oft ausserordentlich grosse Reichtum genotypischer Unterschiede in einer auscheinend einheitlichen Population war von Darwin . . . ebensowenig in der vollen Tragweite erkannt, als es dem grossen Grundleger der Mikrobiologie, Pasteur, klar sein konnte, welche bedeutung es hatte,

³ "Elemente," p. 123.

⁴ On page 121, he remarks on this point: "Selbst die schönste 'typische' Verteilung beweist gar nichts in Bezug auf Einheitlichkeit des derart in Erscheinung tretenden Typus." Professor Johannsen is apparently unaware that this point has been fully recognized by "Biometriker" for years.

dass viele physiologisch sehr differierende Heferassen in vermeintlich 'reinen' Hefekulturen koexistieren konnten.⁵

Proposition 2.—These genotypes are separated generally by differences which are exceedingly minute.

Notwithstanding the constant flood of new species segregated from the classic Linnean groups, necessitating frequent supplements to "Index Kewensis" and other works of its kind, many naturalists could hardly understand the small species discussed by de Vries in his great work. Indeed, many laboratory men hardly perceived the usefulness of recognizing species—perfectly constant, we were assured—so closely related that one taxonomist could not identify the species of another from his descriptions; species so similar that herbarium material was worthless, and only culture side by side could distinguish them. Yet after a lapse of only ten years we find de Vries criticized for not recognizing even smaller divisions than these! Spillman says: "de Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character. . . . They not only do not differ in all their characters as the *Oenothera* mutants do, but their norms present a regular series coming under Quetelet's law."⁶

As examples of these minute differences both he and Lang⁷ quote the "72 Formen einer Population einer gewissen Heferasse" discussed by Nilsson-Ehle.⁸

Jennings says:⁹

The work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurements taken in connection with statistical treatment. Johansen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes of *Paramecium* I found to show constant hereditary differences of one two-hundredths of a millimeter in length. Hanel

⁵ "Elemente," p. 318.

⁶ Spillman, W. J., AM. NAT., 44: 760, 1910.

⁷ Lang, A., Arch. f. Induktive Abstamm.- u. Vererlungsl., 4: 15-16, 1910.

⁸ Nilsson-Ehle, H., Bot. Not., 1907: 113-140.

⁹ Jennings, H., AMER. NAT., 44: 144-145, 1910.

found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable errors of our measures.

Proposition 3.—These genotypes are rigid hereditary units; by a process of mutation one may give rise to another, but selection within the genotype is incapable of effecting a change.

This theory is everywhere so prominent in the writings of the genotypists that discussion or explanation is superfluous.

III. THE CARDINAL PROPOSITION OF THE GENOTYPE THEORY

Of these three essential propositions of the genotype theory of heredity, the first two might be accepted by Darwinian or Lamarckian or by a member of almost any school. If the proposition concerning the exceeding smallness of the differences be true, the theory might seem to present the greatest difficulty to the de Vriesian,¹⁰ for with smaller and smaller genotypes there is a constant approach to continuity, but we are assured that continuity is never realized.¹¹

The third proposition—that genotypic differences are rigid and unchangeable except by mutation—is therefore the essential one. The most obvious way in which this hypothesis can be tested against concrete facts is to determine the effect of selection upon genotypes.

The very heart of the pure line theory is the proposi-

¹⁰ Jennings (AMER. NAT., 44: 145, 1910) tells us, "The genotype work lends no support to the idea that evolution occurs in large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races."

¹¹ Johannsen ("Elemente," p. 356) says in criticism of the Lamarckian theory: "Die Lamarckismus muss kontinuierlich verschiebbare Typen annehmen; wir finden aber bei genauer Prüfung immer und immer wieder Diskontinuität."

tion that selection within the pure line is ineffective.¹² The strenuousness with which this has been maintained has even engendered in some minds the opinion that selection has no rôle at all to play in evolution or in practical breeding. The attitude of many appears to be that Darwin was quite mistaken when he wrote, "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him."

Darwin said, "If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice." Fifty years after this was written we hold a symposium to celebrate the discovery that selection is after all merely the isolation of distinct varieties!

Was Darwin right or wrong? Have all practical breeders except those at the oft-quoted Svalöf station been chiefly occupied in wasting their time for the last fifty years? These are very important questions.

The burden of proof obviously lies on the genotypists.¹³ Much of the evidence offered is most general and not at all *unzweideutig*. Indeed, when closely analyzed much of the reasoning reduces to a circle of three arcs each of one hundred and twenty degrees:

1. *Definition*.—A genotype or biotype is an organic unit, reproducing itself constantly¹⁴ except for the transitory, non-inheritable modifications due to environmental influence.¹⁵ It is not capable of change by selection.

¹² Johannsen ("Elemente," p. 137) states the problem: "Wird Selektion von Plus—oder Minus—Varianten innerhalb reiner Linien eine Typenverschiebung bezw. eine Galton'sche Regression hervorrufen?"

¹³ To be acceptable, the evidence must be quantitative; the observations must either be numerous enough that variations due to uncontrollable factors will average out, or the experiments be conducted with such refined technique that environmental influences are entirely excluded; the statistical reasoning concerning the observations must be logically sound.

¹⁴ "A biotype is a group of individuals which do not differ from one another in any hereditary quality and which therefore constitute a pure race."—Shull, G. H., *Am. Breed. Mag.*, 1: 100, 1910.

¹⁵ "In a given 'pure line' (progeny of a single individual) all detectable

2. *Observation*.—Selection has never been known to produce a change in a genotype. Whenever, as is often the case, selection does result in modification of type this proves that the material considered was impure—that more than one genotype was originally present—or that others arose by mutation, and entirely irrespective of selection.

3. *Conclusion*.—It is therefore proved that selection can not modify the characters of a genotype.

Johannsen has written a very thick and a very convincing-looking book, but if one pins himself down to the task of going from cover to cover he finds that an unfortunate amount of the evidence reduces to this kind of reasoning—in short, to no critical evidence at all.¹⁶ But behind this citing of examples which are not inconsistent with his theory although they prove nothing concerning it; besides this reiteration of testimony which merely excites in the minds of the court-room spectators suspicions concerning the integrity of the defendant without entitling the plaintiff to a verdict before an impartial jury,¹⁷ there are certain direct experimental studies variations are due to growth and environmental action, and are not inherited.”—Jennings, *Proc. Am. Phil. Soc.*, 47: 521, 1908.

“The standard deviation and coefficient of variation express in a pure race mere temporary conditions of no consequence in heredity. If we could make all conditions of growth and environment the same throughout our pure race, all the evidence indicates that the standard deviation and coefficient of variation would be zero, and this is the positive value of their assistance in determining what shall be the characteristics of the progeny.”—Jennings, *AMER. NAT.*, 43: 333, 1909.

“Wenn es gelänge, für alle Individuen einer reinen Linie absolut gleiche Lebenslage zu schaffen, müsste die Standardabweichung gleich sein.”—Römer, T., *Arch. Rassen- u. Gesells.-Biologie*, 7: 437–438, 1910.

¹⁶ For instance, he (“Elemente,” p. 162) refers to the fact that Hallet was unable to improve Le Couteur’s wheat, although he had succeeded in improving seventy other samples from all parts of the world, and explains it by the assumption that in every case the seventy series of wheat were mixtures of biotypes while Le Couteur’s was a pure line. This may be true, but what is it worth as scientific evidence?

¹⁷ In working over the literature of the pure line theory the lover of fair play is sometimes on the verge of losing his patience, for although the experimental data—at least those which are confided to his reader—upon which Johannsen grounds his own theory are very slender, he is unsparing

which have been adduced in support of the genotype theory. These arguments and the evidence upon which they rest must be examined. For convenience of treatment I do this under three propositions concerning selection, which seem so reasonable that I believe few biologists will feel inclined to deny their soundness. They are at least so reasonable that no worker can afford to leave them out of consideration.

A. Characters which are not Inherited at all can not be Taken to Prove that Selection in General is Ineffective

This is a point of great importance, generally ignored by pure-linists. Biometricians have long known that of the variations of any character whatever not all are inherited.¹⁸ They have also learned that variations in certain characters are not inherited.

Suppose now that one takes a character which gives no correlation between its degree of development in

in his criticism of the pioneer studies which have made his own work possible. Such bald statements as ("Elemente," p. 285), "Alle solche Schlüsse sind aber für die eigentliche Erbllichkeitsforschung gänzlich ohne Wert," seem to have little of profit to contribute to science. Johannsen's *ipse dixit* has been taken as gospel. Woltereck (*Verh. Deutsch. Zool. Ges.*, 1909: 115) says, "Dieses Resultat erschüttert ernstlich die Grundlagen der statistischen Variations- und Erbllichkeitforschung, wie sie von der Galton-Pearsonschen Schule betrieben wird." A. Lang (*Verh. Deutsch. Zool. Ges.*, 1909: 24) asserts, "Die biometrischen Forschung arbeitet mit unreinen Material." Römer (*Archiv f. Rossen- u. Ges.-Biol.*, 7: 427, 1910) tells us, "Variabilitätsstudien sind bis in die neueste Zeit meist an Material ausgeführt worden, dessen Einheitlichkeit jeweils als sicher angenommen wurde, das aber nach dem jetzigen Stande der Wissenschaft als unrein angesehen werden muss. Dies tritt besonders hervor bei den veilen Untersuchungen der Biometriker."

¹⁸ This is one of the facts which has led the biometrician to discuss probabilities while biologists in general clamor for certainty in the individual instance. One of the results of recent experimental work that has been hailed with the greatest enthusiasm is that two individuals may be identical in external appearance and yet produce entirely different offspring: in short, that some (somatic) variations are and some are not inherited. The experimental data collected on this point both by pure line and by Mendelian researches are of high value, but those who hail them as novel simply parade their ignorance of much of the pioneer work in variation and inheritance.

parent and offspring in a population and selects to increase or decrease it. He will get no result of selection. If now he takes the same character and selects from the plus and minus variations within a pure line, he will again effect no change by selection. Does either of these cases prove that selection in general is ineffective? Or does the second support in any way Johannsen's genotype theory of heredity? Certainly not.

Certain important work of Pearl and Surface seems to me to deserve mention in this connection.¹⁹ These researches are sometimes referred to as furnishing evidence against the possibility of improvement by selection, and this they do so far as the character with which they have dealt is concerned. In the generalization of their results, however, the greatest caution must be used.

From two series of experiments with the same strain of Barred Plymouth Rock fowls they show that there is little hope of increasing the egg-laying capacity by direct selection for fecundity. These results are doubtless of much practical importance. Biologically they are of interest in confirming the results of other biometric studies which have shown that for man, horse, swine and mice fertility is very slightly inherited in the population. To consider them as indicating that selection in general is ineffective would be a very grave error, for fertility—so far as we may judge from the statistics so far published—seems to be a character *sui generis* in respect to inheritance. To cite these results in support of Johannsen's genotype theory of heredity, as has sometimes been done, is absurd.

Is it not possible that Johannsen's results with beans may be due to seed weight being a character which is not inheritable at all in the population, and which can not, therefore, reasonably be expected to be inherited within the pure line?

¹⁹ Pearl, R., and F. M. Surface, "Inheritance of Fecundity," Bull. Me. Ag. Exp. Sta., 166, 1909. Pearl, R., and F. M. Surface, "Is there a Cumulative Effect of Selection?" *Zeitschr. Ind. Abstamm.- u. Verebungsl.*, 2: 257-275, 1909.

Biologists will agree, I believe, that to test critically the effectiveness of selection in the population and in the pure line, the experimental material must be an apparently homogeneous wild species or a garden variety the individuals of which are not differentiated into sub-races by characters other than those under consideration.²⁰ Conclusions drawn from any experiments in which these simple precautions are neglected seem of doubtful value.

From Professor Johannsen's first memoir, that of 1903, we have no reason to suspect that his material is not, so far as the biologist can judge, homogeneous.²¹ We are told nothing of any vegetative differences seen during the two generations grown in 1901 and 1902. Apparently all the numerous reviewers have considered his material perfectly homogeneous except for differentiation into genotypes with respect to seed characters.

In his book, however, one notes with some surprise the casual information ("Elemente," p. 311) that his Pure Line I also has curiously bent seeds, a special "Verhalten" in germination and a "grobe Håbilus" in the vegetative organs. Indeed Johannsen states that from the form and method of germination, etc., of a seed—even though a strong "minus Abweicher"—he can generally recognize an individual belonging to Line I.

These points should have been made clear at the beginning. If Professor Johannsen's lines really differ in their vegetative characters, so, for instance, that they can be distinguished as they grow in the field, it seems to me that their significance for the efficiency of selection is

²⁰ Surely we can all agree that the population is to be an apparently homogeneous one, *i. e.*, such that all the individuals would be classified together by a keen taxonomist. If this is not the case, if by definition, "population" means to the pure linist a mixture of several conspicuously different things, there seems little need for further discussion.

²¹ Of the seed he says, "Der Ausgangspunkt dieser Untersuchungen war eine gekaufte Partie, etwa 8kg, brauner 'Prinzessbohnen,' wohl eine der ältesten Kruppböhen unten den vielen Kulturformen von *Phaseolus vulgaris*. Die betreffende Ware . . . war ausgezeichnet schön und so gleichmässig, wie es überhaupt hier erwartet werden konnte."

greatly reduced. We do not know to what extent the differences in seed weight which give the low correlation in his population are due to the mixture of races slightly differentiated with respect to their vegetative characters. If this differentiation be considerable, the seed weight character with which Professor Johannsen has chiefly worked, may not be inherited at all in the population providing this population be one composed of individuals with the same vegetative characters. It is not sufficient to be assured that these classic beans differ "nur (oder fast nur)" in seed characters; more detailed information is much needed, and until it is forthcoming I must differ from most biologists in my opinion as to the importance to be attached to the conclusions drawn from them.

B. Improvement for any Single Character can not be supposed to be Unlimited

This is a fundamental consideration too often neglected.²² A wheat is selected up to its maximum productiveness, perhaps by getting the uppermost attainable limit at one choice from a large field. Then because it can not be made to yield all grain and no stubble we are told that selection can only isolate already existing types. A sugar beet can not be all sugar and the cow can not give pure cream.

In arguing for Johannsen's theory East²³ concludes that since Illinois is no longer making progress in high

²² The principle, however, has been clearly seen by some biologists. For instance, in his "Foundations of Zoology," Brooks says (p. 165): "A breeder of domesticated animals or of cultivated plants, who devotes his attention to one or two characteristics, must soon reach a point where no further improvement is practicable unless the species is at the same time greatly modified in many other respects." And again (pp. 177-178), "No one can dispute the well-known fact that this sort of *pedigree selection* for a single point quickly grows less and less effective, and soon reaches a maximum; but this is no proof of any 'principle of organic stability,' or anything else except the truth that long ages of natural selection have made the organism such a unit or coordinated whole that no great and continuous change in one feature is possible unless it be accompanied by general or constitutional change."

²³ East, E. M., "The Rôle of Selection in Plant Breeding," *Pop. Sci. Mo.*, 77: 198-199, 1910.

and low oil and protein selection in maize, their work has been merely the isolation of pure and constant strains—"sub-races"—with the characteristics in question as strongly developed in the beginning as we now find them, but continually intercrossing. The case is too complicated for discussion in detail, but certainly the fact that the characters can no longer be increased by selection²⁴ is no strong argument for the biotype idea. Under its present morphological and physiological organization we have no reason to suppose that the corn grain can be made to contain as much oil as the castor bean.

Again Pearl and Surface²⁵ announce concerning their selection work with corn,

We find the results of this experiment or investigation to be very difficult (if not altogether incapable) of rational explanation in accordance with the biological implications of the "law of ancestral inheritance" and conclude that the results agree better with the genotype theory of Johannsen than with that of the cumulative theory of selection with, of course, the limitations implied by the fact that it is an open fertilized plant.

What Pearl and Surface have actually done is to take a desirable sweet corn which they for convenience designate as Type I, and attempt—with initial success—to improve it for yield in ears and stover, for configuration of ears, and especially for earliness. But this Type I corn is descended from a few ears, the offspring of which have been grown in Maine for fifteen to twenty-five years. The variety originally introduced must have been an

²⁴ That changes due to selection are at first rapid and then slower has long been recognized. Indeed, as early as 1869 Hallett stated as two of his laws of the action of selection, "The improvement which is at first rapid, gradually, after a long series of years, is diminished in amount, and eventually so far arrested that, practically speaking, a limit to the improvement in the desired quality is reached. By still continuing to select the improvement is maintained and practically a fixed type is the result."

Darwin's views on this question are partly expressed in a letter of 1869 to Sir Joseph Hooker ("More Letters," 1: 314), "I am not at all surprised that Hallett has found some varieties of wheat could not be improved in certain desirable qualities as quickly as at first. All experience shows this with animals."

²⁵ Pearl, R., and F. M. Surface, "Experiments in Breeding Sweet Corn," Me. Ag. Exp. Sta. Bull., 1910.

early one as compared with sweet corn in general, to be able to survive at all in Maine. During the fifteen to twenty-five years the ancestors of the Type I corn were grown in Maine it must have been²⁶ subjected to an occasional natural selection, for seed could be taken by the farmers from only plants which had ripened their ears. The somatic organization of some plants is such that they require only a few hours for their life cycle, but so long as sweet corn has the general characteristics of root, shoot and leaf that identify it as *Zea Mays* it seems reasonable to suppose that there is some limit to the reduction of the time required for germination, growth and fruiting—an irreducible minimum beyond which selection can not carry it. Surely the fact that Pearl and Surface could not continually reduce the time required for growth while at the same time maintaining a selection for yield of ears and stover may indicate that the irreducible minimum for earliness has been reached in a variety of the physical type they wish to breed. Speaking for myself alone, I must say that the data before us prove nothing against the theory of cumulative effect of selection, and they certainly do not furnish any critical evidence for the Johannsenian theory.

It seems to me that Pearl and Surface again tacitly make this unjustifiable assumption that the modification attainable for any single character is practically unlimited when they consider that their failure to increase egg production by selection is a legitimate argument against the potency of selection. Indeed they say of "200 egg hens," which lay an egg fifty-five per cent. of the days of the year, "This figure is of some interest as indicating what a *relatively* small proportion of the theoretically maximum character is being selected to, when 200-egg birds are bred."²⁷

But why, pray, is two hundred and sixty-five and a quarter eggs per year the *theoretical maximum*? One

²⁶ Judging from the account of the difficulties of growing sweet corn which the authors give us.

²⁷ Pearl and Surface, Bull. Me. Ag. Exp. Sta., 166: 55.

ignorant of the physiology of reproduction in the domestic fowl might innocently suppose that even a hen needs a rest. If this be true, may it not be that 200 eggs is about the attainable maximum (the physical or physiological limit of the organism) of this variety under the environmental conditions available and that the Maine strain of poultry will not do better than it has? If this is not the attainable limit, why not assume over an egg a day as the theoretical maximum?

C. Selection can not in general carry a Character beyond a Degree Consistent with the Optimum for Maintenance and Reproduction

This proposition is perhaps in a sense explanatory of the one immediately preceding. A characteristic is not independent of, but correlated with the other characteristics of the organism, and if it increases or decreases unduly they must also change or the organism be made more or less unfit for survival.

Have those who claim to have found selection ineffective been selecting against the morphological or physiological balance of the organism, that is in a manner to render the organism less capable of maintenance, growth and reproduction?

If this be true their failure to obtain results will be in some measure explained.

A possible illustration of this case may be furnished by the work of Pearl and Surface on egg production in the domestic fowl. Their work is again chosen not because of any malicious desire to differ from them²⁸ in interpretation, but because in a brief discussion of the evidence for the genotype theory one must confine his attention to the most important of Johannsen's supporters.

The data are: (a) The results of an eight years' selec-

²⁸ The criticism presented here must not be interpreted as drawing into question the scientific value of the data or the practical importance of the results of the studies criticized, or be extended to other work of the same authors, but is to be limited to the question of interpretation in relation to the pure line problem.

tion for high egg production; (b) a correlation between the egg production of thirty-one individual mothers and the egg production of their daughters, and the comparison of the egg production of these daughters with that of a large number of pullets of unregistered female parents.

We note the following details:

1. During the eight-year selection experiment²⁹ some unfavorable environmental accidents occurred in certain of the laying years. The averages for these years are perhaps too low, and both the actual means and a series of corrected means are given. The corrected means show an insignificant increase, but the unmodified means show a pronounced decrease in mean number of eggs as the result of the eight year selection.

2. In correlating between the egg production of the 31 highly selected mothers and their 217 daughters there is not trustworthy evidence of any relationship between the fertility of the mothers and that of their daughters.³⁰ *If these constants show any deviation from 0 whatever it is on the negative side.*

3. In comparing the daughters of these "200-egg" hens with three other series of the same strain but not of such highly selected female parentage, both for winter and spring egg production, it is shown that in five cases out of six the offspring of less highly selected parentage are better layers than those of the less stringently selected parents.

Thus all three comparisons indicate that the high laying mothers tend to produce low laying daughters; selection to increase egg production actually decreases it.

²⁹ "The practise in breeding was to use as mothers of the stock bred in any year only hens which laid between November 1 of the year in which they were hatched and November 1 of the following year, 160 or more eggs. After the first year, all male birds used in the breeding were the sons of mothers whose production in their first laying year was 200 eggs or more. Since the normal average annual egg production of these birds may be taken to be about 125 eggs, it will be seen that the selection practised was fairly stringent." *Zeit. Ind. Abst.- u. Verebungsl.*, 2: 261, 1909.

³⁰ From a knowledge of the biometric work of the last several years this is just the result which one would have expected to get.

Such a run of results as this can hardly be due to chance.³¹ They indicate rather the presence of some as yet undetermined physiological factor.³²

Candidly viewed and considered in comparison with other biometric work on the inheritance of fertility and fecundity, I think these experiments can not be held to be strongly opposed to the theory of the effectiveness of selection in general. However this may be, they certainly afford no substantiation for Johannsen's genotype theory of heredity.

IV. SUMMARY AND CONCLUSIONS

By the genotype theory of Johannsen one understands the following propositions:

An apparently uniform population or phænotype is generally not homogeneous, but is composed of a large number of differentiated types, which are to be designated—within limitations to be laid down immediately—as genotypes.

Externally, the genotype can not be distinguished from the phænotype. Both may have normal variation curves, but while that of the phænotype may by proper selection be broken up into constituent genotypes, the variation curve of the genotype can not be modified by selection. In short, the genotype is from the standpoint of heredity a rigid unit. All individuals belonging to the same genotype have the same potencies as parents. Only discontinuous segregations or transformations—mutations—may modify them.

³¹ The argument that this observed decrease as the result of selection to increase egg production is due to chance must rest chiefly on one or both of two assumptions. First, that the eight-year selection experiment is absolutely untrustworthy because of the accidents which may have affected the egg production in certain years adversely. Second, that 31 mothers is a number entirely too small to give significant results in the case of a character like fecundity. These admissions would vitiate entirely any conclusion concerning selection to be drawn from these experiments.

³² To me it seems that some of Pearl and Surface's published data are most suggestive of the nature of this factor, but they doubtless have in progress experiments that will throw light on these matters and biologists will await their results with interest.

The keystone of the pure line arch is the proposition that selection is ineffective except as a means of separating already existing genotypes. If this keystone-proposition be not sound the whole structure of the theory crumbles.

The propositions of the genotype theory are such that scientific proof or disproof is rendered particularly difficult. By theory selection can not effect a change in a pure line; by a slippery process of reasoning in a circle any results attained by selection are at once discredited by the assertion that the original material was impure. If, on the contrary, any selection experiment is ineffectual it is by some process of reasoning quite incomprehensible to some of us, at once chalked up to the credit of the new theory. If heritable differences appear within a pure line known to be so, these results are also discredited by the assertion that the observed change is a mutation or has been produced by the action of the environment. Truly the unbiased investigator is between the devil and the deep sea!

The actual experimental data upon which the genotype theory rests are as yet few. Johannsen's conclusions for beans depend chiefly upon the offspring of only nineteen seeds, and so far as I am aware no other investigator has confirmed his results on *Phaseolus*. Hanel had only twenty-six original *Hydra*, and Pearson's analysis of his data with more adequate methods than he used, evidences against rather than for the genotype theory. Jennings gives us the records of only six selection experiments involving altogether only a few actually selected *Paramecia*. Considering the large environmental and growth factors, his conclusions can not be considered as beyond question.³³ The work of Pearl and Surface with poultry and maize seems to me to have

³³ In offering this criticism I wish to express the highest admiration for Professor Jennings's two memoirs on variation, heredity and evolution in the protozoa. The coupling of refined statistical with careful experimental methods in the investigation of these organisms marks a great advance in biology.

no critical bearing on the pure line problem.³⁴ This is also true of numbers of other smaller experiments which can not be cited.

If one turns from the strictly pure line side of the problem to the more general questions of the "something" or "Etwas" in the germ plasm which determines in large degree the somatic characters of the individual which develops from it, one can only suggest that nothing whatever is explained by giving another name to a well-known fact. Ever since the time of Darwin, and before, we have known that there was "something" in the germ cells which determined the character of the offspring. We have had a dozen different names for this something, and by adding a thirteenth, "Gene," Johannsen has merely burdened us with another cloak for our ignorance. Unfortunately biological closets are full of such cloaks, once in fashion—now out.

Finally, I must make my own position quite clear. With Professor Jennings's contention that pure line cultures are of fundamental importance in many fields of physiology and genetics, I am in hearty agreement. Like other breeds of facts, "pure line facts" can not become too abundant. Indeed, *a priori*, I am not opposed to the genotype theory. As a theory it is most attractive, but one can not accept it without proof on that account. Personally, I am one of "that last small remnant" who believe that in a problem of this kind the proof must be biometric. This means merely three things. In so far as the nature of the material permits, all the data considered must be quantitative. The data must be numerous enough that biological relationships will not be obscured by the errors of random sampling. The data must be analyzed by logically sound methods.

Judged by these standards, I must express the conviction that as yet there is no adequate justification for the genotype or pure line theory.

³⁴ Naturally, this is purely a matter of interpretation, and does not diminish in the slightest degree the value of the work.